HISTOLOGY OF THE RETRACTOR MUSCLES OF PHASCOLOSOMA GOULDII POURTALÈS

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Although much work has been done on the detailed anatomy of the invertebrates, very little more than incidental and superficial descriptions of the musculature have been given. Inasmuch as many invertebrate muscles are being used in physiological and biophysical research, it seems important that a knowledge of their detailed histology be made available. As I indicated in a previous paper (Olson, 1938), histological studies of the muscles of the invertebrate series may also reveal facts of possible phylogenetic significance.

I have found in the literature no previous detailed histological studies of the retractor muscles of *Phascolosoma* although Gerould (1906) mentions the formation of muscle fibers in his description of the development of *Phascolosoma.* Descriptions of muscles of related forms (Graff (1875), on *Chaetoderma;* Andreae (1881), on *Sipunculus nudus;* Apel (1885), on *Priapulus* and *Holicryptus;* and Jameson (1899), on *Thalassema*) present quite a different histological picture.

Materials and Methods

The retractor muscles of *Phascolosoma* consist of two pairs of flattened bands which extend from the front end of the base of the introvert to the body wall. They are 3–5 mm. in width and 1–2 mm. in thickness. They vary in length from 1–1.5 cm. in normal contraction to 7–10 cm. in normal extension. The ventral retractors are somewhat longer than the dorsal, being attached 3–5 mm. posterior to them. They are also somewhat thicker.

The muscles were fixed in varying states of contraction in Bouin's and Helly's fixing fluids. They were dehydrated in Dioxan, imbedded in paraffin, and sectioned at 5 and 10 micra. The sections were stained with Heidenhain's iron haematoxylin, Mallory's phosphotungstic acid haematoxylin, and Dominici's staining mixture.

The muscles were successfully macerated in 10 per cent nitric acid. It was thus possible to obtain free fibers and to measure fiber lengths.

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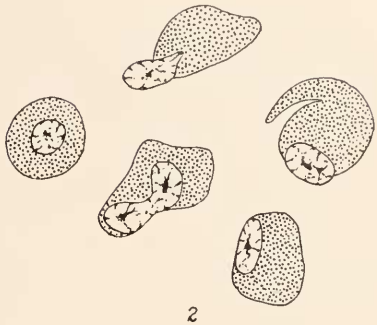

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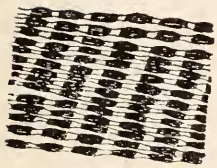

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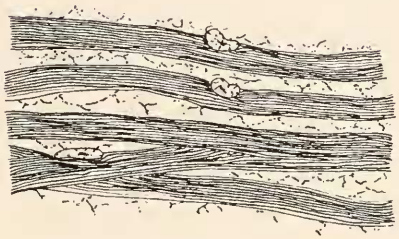

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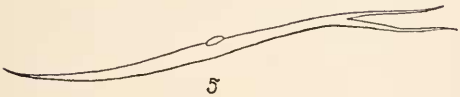

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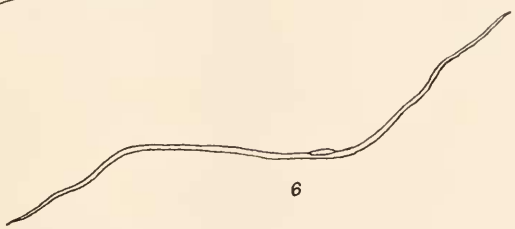

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Explanation of Figures

All drawings were made with the aid of a camera lucida.

Fig. 1. Cross-section of a small portion of a muscle showing fibers, fibrils, and distribution of connective tissue. × 625.

Fig. 2. Cross-section of individual fibers showing the position of the nuclei. × 1250.

Fig. 3. Longitudinal section of a portion of a muscle fixed in isometric contraction showing the cross-striations produced by the vertical alignment of the contraction nodes of adjacent fibers. × 168.

Fig. 4. Longitudinal section of a portion of a resting muscle showing fibers, fibrils, fiber nuclei, and the distribution of the connective tissue. × 625.

Fig. 5. A contracted branched fiber from a preparation of macerated muscle. × 63.

Fig. 6. A typical resting fiber from a preparation of macerated muscle. × 63.

Results

The retractor muscles of *Phascolosoma* consist of comparatively densely packed spindle-shaped fibers which in the resting state have an average length of about 1 mm. and a maximum length of about 1.5 mm. The fibers vary in diameter from 3 or 4 micra up to 20 micra with an average diameter of about 6 or 7 micra. In cross-section the fibers may appear cylindrical, hemicylindrical, or angular. Occasional branched fibers are also found (Cross-section, Fig. 2; single fiber from teased muscle, Fig. 5).

The fibers are uninucleate, the nuclei occupying a position similar to the nuclei of vertebrate smooth muscle midway between the terminals of the fibers (Fig. 6). Unlike the nuclei of vertebrate smooth muscle, however, they usually have an eccentric position within the fiber (Fig. 2). Occasional nuclei are found in a central position, a few others peripheral to the fibrillar zone.

The contractile elements are densely packed fibrils uniformly distributed throughout the fiber, and not peripherally arranged as in *Thalassema* (Jameson, 1899), *Sipunculus* (Andreae, 1881), *Priapulus* and *Holicryptus* (Apel, 1885). They are essentially straight parallel structures as described by Keferstein (1865), and in no instance show the spiral structure described by Jameson for *Thalassema*. The fibers fail to show the multiplicity of zones described for the muscle cells of other sipunculids. A central canal, an area of fibril-free sarcoplasm, can not be demonstrated. The description by Jameson of radially arranged contractile plates in the cortical layer and an outer hyaline layer bounding the sarcolemma externally could likewise not be substantiated in a study of the retractor muscles of *Phascolosoma*.

The muscle fibers do not show a definite arrangement into bundles as do the retractor muscles of *Thyone* (Olson, 1938). The proportion of connective tissue and tissue space is also considerably smaller than in *Thyone*. As in the retractor muscles of *Thyone*, however, each fiber is invested by connective tissue which forms a delicate reticulum connecting adjacent fibers (Figs. 1 and 4).

A curious phenomenon not previously reported for invertebrate muscle is the cross-banded appearance of the muscle fixed in a state of isometric contraction (Fig. 3). The "striations" are visible only in muscles fixed in isometric contraction; the resting and isotonically contracted muscles do not show them. The cross-banded muscles resemble the so-called striated muscles which Carey (1921, 1924) claims to have produced experimentally in the bladder of dogs. Jordan (1938), however, believes the simulacra of cross-striations seen by Carey to have

been produced by the alignment of contraction nodes, or in some instances, by the folding and buckling of the fibers. In the retractor muscles of *Phascolosoma* likewise, the dark and light bands can scarcely be homologized with the Q and J discs of striated muscle since they exceed in relative size the discs of any type of striated muscle, and further, do not show the characteristic Z membranes or M discs. They are best interpreted as being formed by the alignment of the contraction nodes of adjacent fibers, and inherently by the vertical alignment of the darkly stained areas of the fibrils within each muscle cell. However, the very fact of the precise alignment and the uniformity of the nodes suggests a primitive or simplified type of striated muscle or a transition type in a possible evolution of striated from smooth muscle. Hursh (1938) found that *Phascolosoma* retractor muscles, much as striated muscles, respond well to electrical stimulation and are able to shorten from one-sixth to one-seventh of their original length. The final interpretation, however, must await additional physiological data for corroboration.

Summary

The retractor muscles of *Phascolosoma* consist of densely packed spindle-shaped fibers which have an average length of 1 mm. and an average diameter of 6 or 7 micra.

The fibers are uninucleate, the nuclei usually occupying an eccentric position midway between the fiber terminals.

Fine fibrils are densely and uniformly distributed throughout the fibers. They are essentially straight parallel structures.

Vertical alignment of the contraction nodes of adjacent fibers in isometrically contracted muscle produces cross-striations simulating the Q and J discs of skeletal muscle.

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